ZOFIA KIELAN-JAWOROWSKA

EVOLUTION OF THE THERIAN MAMMALS IN THE LATE CRETACEOUS OF ASIA. PART V. SKULL STRUCTURE IN ZALAMBDALESTIDAE

(Plates 14—17)

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The Late Cretaceous specialized proteutherian family Zalambdalestidae embraces 3 monotypic genera: *Zalambdalestes*, *Barunlestes* and (tentatively assigned) *Daulestes*. Zalambdalestid skull is characterized by: strongly elongated, narrow snout, with a long diastema between I^3 and C; zygomata slender, strongly expanded laterally; brain case more inflated and mesocranial region shorter than in contemporaneous proteutherians; occipital plate inclined forwards from the condyles; maxilla extending backwards along the choanae; presphenoid with prominent median process; large pterygoid process of basisphenoid; f. rotundum; groove for chorda tympani; postglenoid process extending only opposite medial part of glenoid fossa; large promontorium, f. arteriae stapediae, sulcus arteriae stapediae, no sulcus arteriae promontorii; lambdoidal crests prominent. The zalambdalestid skull is more specialized than those of *Kennalestes* and *Asioryctes* which occur in the same beds and shows a mosaic of primitive and advanced characters.

Key words: Mesozoic mammals, skull structure, Eutheria, Cretaceous, Zalambdalestidae.

Zofia Kielan-Jaworowska. Zakład Paleobiologii, Polska Akademia Nauk, 02-089 Warszawa, al. Żwirki i Wigury 93, Poland, *Received: June, 1981.*

EWOLUCJA SSAKÓW THERIA W PÓŹNEJ KREDZIE AZJI. CZĘŚĆ V. BUDOWA CZASZKI ZALAMBDALESTIDAE

Streszczenie. — Wyspecjalizowana rodzina późno-kredowych ssaków łożyskowych Zalambdalestidae obejmuje 3 monotypowe rodzaje: *Zalambdalestes*, *Barunlestes* i *Daulestes* (zaliczony z zastrzeżeniem). Czaszka przedstawicieli Zalambdalestidae charakteryzuje się wąskim, silnie wydłużonym pyskiem, długą diastemą między I^3 i C, cienkimi, silnie wygiętymi na boki łukami jarzmowymi, puszką mózgową bardziej rozdętą i regionem mezokranialnym krótszym niż u współczesnych im przedstawicieli Proteutheria, tarczą karkową skierowaną od kłykci potylicznych skośnie ku przodowi, obecnością otworu okrągłego i szczeliny dla struny bębenkowej, krótkim wyrostkiem zapanewkowym, rozciągającym się tylko naprzeciw wewnętrznej części dołu żuchwowego, dużym promontorium, obecnością arteria stapedia i brakiem arteria promontorii. Czaszka u przedstawicieli rodziny Zalambdalestidae jest bardziej zaawansowana niż u rodzajów *Kennalestes* i *Asioryctes*, które występują w tych samych warstwach i wykazuje mieszaninę cech prymitywnych i cech specjalizacji.

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INTRODUCTION

The present paper is devoted to the description of the skull structure of the specialized Late Cretaceous eutherian family Zalambdalestidae GREGORY and SIMPSON, 1926. In two specimens of *Zalambdalestes lechei*, the skull of which is described herein, partial endocaranial casts have been preserved. These are described separately (KIELAN-JAWOROWSKA 1984).

The family Zalambdalestidae consists of 3 monotypic genera: *Zalambdalestes*, represented by *Z. lechei* GREGORY and SIMPSON, 1926; *Barunlestes*, represented by *B. butleri* KIELAN-JAWOROWSKA, 1975; and tentatively assigned *Daulestes*, represented by *D. kulbeckensis* TROFIMOV and NESOV, 1979 (*in* NESOV and TROFIMOV 1979). The lower jaw of *Zalambdalestes* has been described by KIELAN-JAWOROWSKA and TROFIMOV (1981), the dentition by KIELAN-JAWOROWSKA (1969), the molar occlusion by CROMPTON and KIELAN-JAWOROWSKA (1978), the skull structure of *Barunlests* by KIELAN-JAWOROWSKA (1975) and KIELAN-JAWOROWSKA and TROFIMOV (1980). These descriptions are not repeated here. Similarly the photograps and drawings of *Zalambdalestes* and *Barunlestes* published earlier are not refigured.

During the preparation of this paper I benefited from discussions with Dr. ROBERT PRESLEY (Department of Anatomy, University College, Cardiff), who offered valuable suggestions. The following persons from the staff of the Institute of Paleobiology, Polish Academy of Sciences helped me in preparation of this paper: Ms. ELŻBIETA GUTKOWSKA made the drawing from my pencil sketch; Ms. JOANNA SKARŻYŃSKA skillfully prepared the described specimens; Mr. WOJCIECH SICIŃSKI arranged the plates. I wish to express my sincere gratitude to all these persons.

I use the following abbreviations:
AMNH — The American Museum of Natural History, New York
PIN — Palaeontological Institute, USSR Academy of Sciences, Moscow
ZPAL — Institute of Paleobiology, Polish Academy of Sciences, Warsaw

DESCRIPTION

Order **Proteutheria** (ROMER, 1966), NOVACEK, 1977
Family **Zalambdalestidae** GREGORY and SIMPSON, 1926

Revised diagnosis. — Comparatively large proteutherians, length of the skull varying between 40 and 50 mm. Skull constricted in front of P^1, with very long, narrow snout. Brain case more inflated than in other contemporaneous proteutherians, zygomata slender, strongly expanded laterally, post-orbital constriction present, occipital plate inclined forwards from the condyles. Sagittal and lambdoidal crests present. Palate without fenestrae, posterior palatine foramina very large, oval. Maxilla extending backwards along the choanae, the presphenoid with a prominent median process, foramen rotundum, very large pterygoid process of basisphenoid, fissura for chorda tympani, postglenoid process extending only opposite the medial part of the glenoid fossa, foramen arteriae stapediae, sulcus arteriae stapediae, no sulcus arteriae promontorii. Dental formula: $I\frac{3}{3}\ C\frac{1}{1}\ P\frac{3-4}{3-4}\ M\frac{3}{3}$; I^2 enlarged, caniniform, I^3 small. Long diastema between I^3 and C. Upper canine very large, placed behind premaxillary-maxillary suture, P^1 small or absent, P^2 small, P^3 tallest of all teeth, with spur-like protocone, P^4 with protocone developed as in molars, but without metacone. Upper molars without cingula, strongly elongated transversely, M^3 small, I_1 enlarged, procumbent, I_2, I_3 and C small, styliform,

P_1 trenchant, P_2 trenchant or absent, P_3 with unbasined heel, P_4 with three cusped trigonid and unbasined talonid. Molars with small trigonids, paraconid and metaconid connate at bases. Long spinous process of the axis, sacrum of 2 vertebrae, scaphoideum and lunatum fused as scapholunatum, tibia and fibula strongly fused, calcaneal fibular facet lacking, tibial trochlea on astragalus well developed, hind limbs (especially metatarsals) very long. The length ratio of forelimb to hindlimb resembles that of present-day Macroscelididae (see EVANS 1942).

Genera assigned: *Zalambdalestes* GREGORY and SIMPSON, 1926, *Barunlestes* KIELAN-JAWOROWSKA, 1975, ?*Daulestes* TRIFIMOV and NESOV, 1979.

Stratigraphical and geographical range. — Late Cretaceous, uncertain occurrence in the Late Turonian „Taykshirskaya pačka" (group of beds) Central Kyzyl Kum Desert, Uzbek SSR; and the following formations and localities in the Gobi Desert, Mongolian People's Republic: Djadokhta Formation (?late Santonian and/or ?early Campanian) of Bayk Dzak; Toogreeg beds (stratigraphic equivalent of the Djadokhta Formation) of Toogreeg; Barun Goyot Formation (?middle Campanian) of the Nemegt Basin and red beds of Khermeen Tsav (stratigraphic equivalent of the Barun Goyot Formation) of Khermeen Tsav II [1].

Discussion. — SZALAY and MCKENNA (1971) included the Paleocene genus *Praolestes* MATTHEW, GRANGER and SIMPSON, from Mongolia in the Zalambdalestidae. *Praolestes* is represented by a single species, known from a single left lower jaw with P_3—M_1. In the Cretaceous Zalambdalestidae there is a tendency towards enlargement of the talonid of P_4, which in *Barunlestes* is slightly larger than in *Zalambdalestes*. In *Praolestes* the talonid of P_4 is relatively smaller than in *Zalambdalestes*. In molars of *Zalambdalestes* and *Barunlestes* the trigonids are greatly reduced in length with respect with the talonids, which is not the case in M_1 of *Praolestes*. Thus *Praolestes* does not seem to be in the evolutionary line deriving from known Cretaceous Zalambdalestidae. Because of this *Praolestes* cannot be placed in Zalambdalestidae with any certainty.

Genus *Zalambdalestes* GREGORY and SIMPSON, 1926

Type species: *Zalambdalestes lechei* GREGORY and SIMPSON, 1926, the only known species.

Diagnosis and distribution. — As for *Z. lechei*.

Zalambdalestes lechei GREGORY and SIMPSON, 1926
(pls. 14—17; fig. 1)

1926. *Zalambdalestes lechei* GREGORY and SIMPSON: 14, figs. 1E—G, 13—18.
1928*a*. *Zalambdalestes grangeri* SIMPSON: 2, figs. 1—2, 4—6.
1928*b*. *Zalambdalestes grangeri* SIMPSON; SIMPSON: fig. 1A.
1961. *Zalambdalestes grangeri* SIMPSON; VANDEBROEK: pl. 10A.
non 1964. *Zalambdalestes grangeri* SIMPSON; VAN VALEN: fig. 2.
1969. *Zalambdalestes grangeri* SIMPSON; KIELAN-JAWOROWSKA: 186, fig. 4, pls. 26 : 1, 27.
1969. *Zalambdalestes* sp.; KIELAN-JAWOROWSKA: 189, pl. 26 : 2.
1969. *Zalambdalestes lechei* GREGORY and SIMPSON; KIELAN-JAWOROWSKA: 173.
1971. *Zalambdalestes lechei* GREGORY and SIMPSON; SZALAY and MCKENNA: figs. 31—35.
1975. *Zalambdalestes lechei* GREGORY and SIMPSON; KIELAN-JAWOROWSKA: fig. 2A.
1978. *Zalambdalestes lechei* GREGORY and SIMPSON; CROMPTON and KIELAN-JAWOROWSKA: 268, figs. 9 and 10.

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[1] The ages of the Djadokhta and Barun Goyot formations given herein follow GRADZIŃSKI *et al.* (1977). When this paper was submitted to publication a paper by KARCZEWSKA and ZIEMBIŃSKA-TWORZYDŁO (1983) was published. These authors argued on paleobotanical evidence that the Nemegt Formations is not younger than the equivalent of the early Campanian stage. It follows that the Barun Goyot Formation, which underlies conformably the Nemegt Formation, may be of ?late Santonian age and the Djadokhta Formation of ?early Santonian or ?late Coniacian age. These estimates should be regarded, however, as tentative.

1979. *Zalambdalestes lechei* GREGORY and SIMPSON; KIELAN-JAWOROWSKA: 6, figs. 1, 3, 8B, 15, 16a, 17, pls. 1 : 2, 3, 4 : 2, 9 : 1, 10 : 2, 11: 3—4.

1981. *Zalambdalestes lechei* GREGORY and SIMPSON; KIELAN-JAWOROWSKA and TROFIMOV: 3, pls. 1—2.

Diagnosis. — Length of the skull ca. 50 mm. Lower jaw slender, coronoid crest without basal swelling. Four upper and lower premolars. Upper canine very large, double-rooted, situated ca. 3 mm to the rear of premaxillary-maxillary suture.

Material

Upper Cretaceous, Djadokhta Formation, Bayn Dzak, Gobi Desert

AMNH 21708 holotype, large part of skull of an old individual, associated with partial left and right lower jaw, figured by GREGORY and SIMPSON (1926), figs. 1E, 13 and 14, and by SZALAY and MCKENNA (1971), figs. 31 and 32.

AMNH 21704, nearly complete skull of an old individual, associated with both lower jaws, figured by GREGORY and SIMPSON (1926), figs. 1G, 17 and 18.

AMNH 21707, fragment of the right lower jaw with P_3—M_3, figured by GREGORY and SIMPSON (1926), figs. 1F and 15, and by SZALAY and MCKENNA 1971, fig. 33.

AMNH 21709 (holotype of *Z. grangeri*), most of the facial portion of the skull with right cheek teeth of an old individual, associated with fragment of the right lower jaw and with partial pelvis and femur. Figured by SIMPSON (1928*a*), figs. 1—6, by VANDEBROEK (1961), pl. 10A (reversed) and by SZALAY and MCKENNA (1971), figs. 34—35.

ZPAL MgM-I/4, (*Zalambdalestes* sp. of KIELAN-JAWOROWSKA 1969), incomplete right lower jaw of a young individual, with alveoli of I_1—C, broken off P_1 and P_2—M_1, figured by KIELAN-JAWOROWSKA (1969), pl. 26 : 2.

ZPAL MgM-I/13, badly damaged anterior portion of the skull of an old individual, with lower jaws in occlusion, figured in this paper: pl. 17.

ZPAL MgM-I/14, well preserved anterior portion of the skull of an young individual, with right and left lower jaws in occlusion, and cast of olfactory bulbs, figured by KIELAN-JAWOROWSKA (1969) as *Z. grangeri*, pls. 26 : 1, 27 : 1, by KIELAN-JAWOROWSKA *et al.* (1979), fig. 12-2.A_3, and in the present paper pl. 16 : 2.

ZPAL MgM-I/15, fragment of left lower jaw with badly damaged M_1—M_3.

ZPAL MgM-I/16, incomplete skull with nearly complete upper dentition, anterior portion of the face lacking, cranial roof badly damaged and partial endocranial cast preserved; lower jaws not preserved. Figured by KIELAN-JAWOROWSKA (1969) as *Z. grangeri*, pl. 27 : 2, by KIELAN-JAWOROWSKA *et al.* (1979), fig. 12—2.A_1, and in the present paper, pl. 16 : 1

ZPAL MgM-I/30, badly damaged rostral fragment of the skull with worn out right and left P^3—M^1 and fragments of right and left lower jaws.

ZPAL MgM-I/31, partial left lower jaw with strongly damaged M_2-M_3.

ZPAL MgM-I/32, fragment of the right lower jaw with damaged M_1-M_3.

ZPAL MgM-I/43, incomplete right and left maxillae with P^3-M^3, associated with nearly complete right and left lower jaws and large parts of the postcranial skeleton. Postcranial skeleton described and figured by KIELAN-JAWOROWSKA (1979), figs. 1, 15, 17, pls. 1 : 2, 9 : 1 10 : 2, 11 : 3, 4; dentition figured by CROMPTON and KIELAN-JAWOROWSKA (1978), figs. 9 and 10; left lower jaw by KIELAN-JAWOROWSKA *et al.* (1979) fig. 12—2.A_2, maxillae, lower jaws and dentition in the present paper, pls. 14 and 15.

ZPAL MgM-I/51, right lower jaw with incomplete angular process, broken I_1 and I_3, root of I_2 and C—M_3, figured by KIELAN-JAWOROWSKA and TROFIMOV (1981), pl. 2 : 2.

ZPAL MgM-I/66, second to seventh cervical vertebrae and first thoracic vertebra, preserved together, figured by KIELAN-JAWOROWSKA (1979), fig. 3, pls. 3 and 4 : 3.

ZPAL MgM-I/167, fragment of left maxilla with P^2—M^1.

Toogreeg beds, Toogreeg, Gobi Desert

PIN 3143-501 nearly complete left lower jaw of an adult individual, with broken incisors, C, roots of P_1—P_2 and P_3—M_3, figured by KIELAN-JAWOROWSKA and TROFIMOV (1981), pls. 1 and 2 : 1.

Skull as a whole.

The snout is very narrow anteriorly, markedly elongated, almost parallel-sided, widening laterally opposite P^3; long diastema between I^3 and C; the zygomata are slender, together forming a rough circle; the brain case is relatively more expanded than in *Kennalestes* and

Asioryctes, sagittal crest short, lambdoidal crests prominent; the mesocranial region is relatively shorter than in *Kennalestes* and *Asioryctes*; the occipital plate is inclined forwards from the condyles as in *Kennalestes* and *Asioryctes*. The most anterior part of the snout is not preserved in any of the specimens, so the presence of the first upper incisors is not certain. Length of the skull varies around 50 mm. It should be explained that in the reconstructions based on juvenile specimens in ZPAL collection (KIELAN-JAWOROWSKA 1975, fig. 2A and 1979, fig. 17) the skull measures 43 mm. The skull of ZPAL MgM—I/16 in which the endocranial cast is preserved measures 46 mm. The skull of the holotype specimen AMNH 21708 measures ca. 50 mm and such are the dimensions of the skull reconstructed in fig. 1.

Snout and zygoma. The nasals are narrow anteriorly, expanded posteriorly contacting the lacrimals. The anterior part of the snout (premaxilla) is insignificantly inflated laterally, in respect to the narrower maxillary part. The premaxilla is long, directed nearly vertically and has an elongted nasal process, with its postero-superior point above the canine. The maxilla is extensive, elongated and has a thickened and concave posterior edge. The infraorbital foramen is ca. 1.5 mm deep, situated above P^2—P^3 embrasure. The length of the infraorbital canal is equal to that of P^3—P^4; the anterior edge of the orbit is situated above the P^4—M^1 embrasure. The suture between maxilla and jugal is not recognized with full certainty. The zygomatic arch starts above the posterior part of M^2. In ventral view the posterior margin of the maxilla is strongly concave, forming an arch between the buccal margin of M^3 and the inner edge of the zygomatic arch. Along the part of the jugal bone which contacts maxilla, a prominent rounded ridge forms the anterior margin of the orbit. It cannot be stated with certainty whether this ridge continues onto the lacrimal. Posteriorly the jugal continues as a slender zygomatic arch. In lateral view the zygomatic arch is sigmoid. The suture between the jugal and squamosal, well preserved on the right side of ZPAL MgM-I/16 (see KIELAN-JAWOROWSKA 1969, pl. 27 : 2), is situated far posteriorly, most of the zygomatic arch being formed by the jugal. The edges of the lacrimal cannot be recognized with full certainty; however, there is a comparatively large facial wing. The lacrimal foramen was not found in ZPAL specimens, but GREGORY and SIMPSON (1926 : 18) stated: "The lacrymal rim is much elevated and sharp, the lacrymal foramen inside the rim".

Palate. Palatal processes of premaxillae are preserved partly in ZPAL MgM-I/14 and/16 and more completely in AMNH 21708. In the latter the suture between premaxilla and maxilla is well preserved. The maxillae taper together anteriorly to a pointed end, inserted between the premaxillae. Palatal processes of maxillae are slightly concave, more so anteriorly than in the molar region, where they widen considerably. The greater palatine foramen is situated opposite the protocone of P^3 and provided with a very short, shallow palatine groove, ending in front of P^3. The shape of the transverse part of the palatine bone cannot be recognized with full certainty. The shape of the cracks in the posterior part of the hard palate in ZPAL MgM-I/14 and/16 suggests that the horizontal part of the palatine tapers anteriorly opposite P^4. The lesser palatine foramen cannot be discerned with any certainty. In *Barunlestes* (see KIELAN-JAWOROWSKA and TROFIMOV 1980) it is situated immediately to the rear of the palatino-maxillary suture, opposite P^4—M^1 embrasure. It is here reconstructed in the same position in *Zalambdalestes* (fig. 1). The posterior palatine foramina are large, oval openings, situated at the posterolateral corners of the transverse part of the palatine bone. They communicate directly with the pterygopalatine fossa, opposite the anterior part of the choanae; posterior palatine canals are not developed. The postpalatine torus is very faint, developed only laterally, while in the middle it widens anteriorly and becomes confluent with the remaining portion of the palatine bone.

Choanae and basicranium. The choanae are very narrow and deep. The nasopharyngeal duct narrows slightly posteriorly. The perpendicular parts of the palatine bones form the walls of this duct and are somewhat convex internally. The maxilla also has a backward extension along the side of the palatine. The shape of the pterygoid bone, with a pointed anterior end,

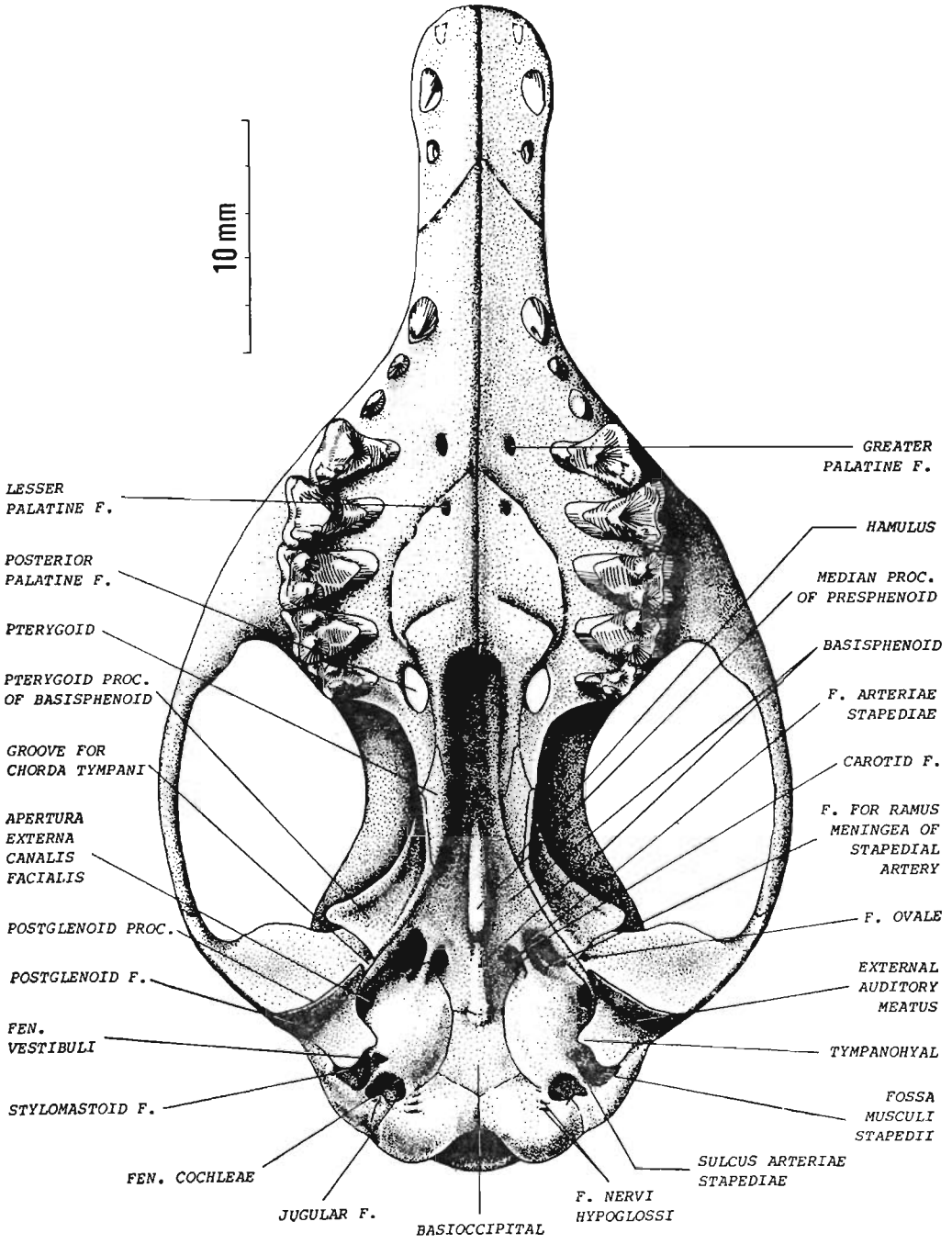

Fig. 1

Reconstruction of the skull of *Zalambdalestes lechei* in ventral view, based in part on the structure of *Barunlestes butleri*.

inserted between the prolongations of the maxilla and palatine, is reconstructed in fig. 1 on the basis of comparisons with *Barunlestes*. The vomer is not discernible, but in the posterior part of the choanal channel a single bone protrudes ventrally as in *Barunlestes*. It is interpreted as a median process of presphenoid. The basicranium is not preserved. Its reconstruction given in fig. 1 is based on the structure of *Barunlestes*.

Cranial roof. The cranial roof is best preserved in AMNH specimens; however, even there, sutures are not discernible. The infraorbital constriction is conspicuous. To the rear of the constriction

the brain case is gently inflated, more so in a horizontal than in a vertical sense. The postorbital process is apparently lacking. The sagittal crest is short but distinct, extending for about 1/8 of the skull's length; the lambdoidal crests are prominent.

Occiput. — In addition to the AMNH specimens a partial occiput is preserved in ZPAL MgM-I/16, which is of a young individual preserving the sutures in this region (pl. 16 : 1b). The supraoccipital is delimited by vertically directed sutures from the mastoids and by roughly transverse sutures (convex upwards) from the exoccipitals. The posterior margin of the supraoccipital is strongly notched for a pointed upper end of the foramen magnum. The supraoccipital is perforated by an unestablished number of small foramina, which as the mastoid foramina (see below) are interpreted as connected with the sigmoid sinus. The exoccipital is roughly semicircular, with concave inner margin. A small fragment of occipital condyle is preserved on the right side, a larger on the left. The condyle is moderately convex, not very prominent and separated from the upper part of the supraoccipital-exoccipital suture. The lower part of the condyle and basioccipital are not preserved. Fragmentary right and left mastoids are preserved. In the upper part of the left mastoid two small foramina are preserved, here called the lower mastoid foramen (LMF) and upper mastoid foramina (UMF), situated above and lateral to the former (pl. 16 : 1b). It is difficult to decide which of these foramina corresponds to the mastoid foramen recognized by COPE (1880), but probably both are related to the sigmoid sinus.

Orbit and temporal fossa. — The orbit is very large, widely open posteriorly and confluent with the temporal fossa. Sutures within the orbit are hardly discernible. In the anterior part a large, roughly triangular floor (maxillary recess) is perforated by numerous foramina alveolaria posteriora, in which fragments of molar roots are visible. Between the horizontal and vertical walls of the orbit is a longitudinal groove, narrowing somewhat anteriorly, similar to that in *Didelphis*. At the posterior end of the groove, opposite M^2—M^3 embrasure, there is a small foramen, recognized as a sphenopalatine foramen (pl. 16 : 2c SPHF). At the anterior end of and laterally to the groove is a maxillary foramen (MF). Posterolaterally to the sphenopalatine foramen is the large oval opening of the posterior palatine foramen (PPF). Along the outer margin of the groove, well visible on the right side of ZPAL MgM-I/14, is the suture separating the maxilla from the palatine. The maxilla does not appear to extend into the medial wall of the orbit. The anterior part of the orbit in *Zalambdalestes* shows great similarity to that in *Didelphis*. The similarities are: the presence of this groove, the position of maxillary and sphenopalatine foramina at either ends of the groove and presence of posterior palatine foramen, piercing the maxilla, situated posterolaterally with regard to the sphenopalatine foramen.

The exposure of the remaining bones in the orbit and temporal fossa, and position of foramina cannot be recognized with any certainty. In ZPAL MgM-I/14, a part of the ethmoid bone is visible. The skull is broken at the posterior end of olfactory bulbs. In posterior view, below the endocranial mould of the olfactory bulbs, a roughly trapezoidal plate, oriented obliquely downwards is recognized as the posterior part of the cribriform plate (pl. 16 : 2c). The anterior part of the cribriform plate, housing the olfactory bulbs, is not visible. The posterior part consists of right and left portions, joined in the middle by a rounded ridge. Posteriorly the ridge bifurcates, passing into transversely directed ridges, surrounding the plate from behind; the lateral margins of the plate are not preserved. Each (right and left) part of the plate is concave and perforated by small foramina (about 30 on the right side). To the rear to the plate only the matrix is preserved and the contact with orbitosphenoid cannot be traced. In the anterolateral corners the preserved part of the cribriform plate joins the cranial part of the frontals.

In most Recent mammals the cribriform plate consists of two ethmoidal fossae, with a median ridge between them. The ethmoidal fossae are perforated by comparatively large, characteristically arranged foramina. The posterior margin of ethmoidal fossae joins the orbitosphenoid. However, in *Didelphis* there is a quadrangular posterior prolongation of the cribriform plate,

perforated by foramina which are much smaller than the foramina in the ethmoidal fossae. The plate in *Zalambdalestes* is regarded as corresponding to the posterior prolongation of the lamina cribrosa in *Didelphis*. In *Zalambdalestes* it is more vertical than in *Didelphis*, which may be partly caused by the state of preservation.

Glenoid fossa. — The glenoid fossa is preserved in AMNH specimens and in ZPAL MgM-I/16. It forms a comparatively large, roughly oval plate, transversely elongated, nearly flat, horizontally arranged. Anterior margin of the fossa is convex, lateral margin passes into the fine zygomatic arch. The postglenoid process surrounds the fossa only posteromedially, the posterolateral edge of the fossa has no rim and is slightly bent downwards.

Lower jaw. See pls. 14 : 1a—1c and 15, and KIELAN-JAWOROWSKA and TROFIMOV (1981: pls. 1 and 2).

Dentition. See pls. 14, 15 and 17 and KIELAN-JAWOROWSKA (1969 : 186, fig. 4 and pls. 16, 17) and CROMPTON and KIELAN-JAWOROWSKA (1978 : 268, and figs. 9 and 10).

Genus *Barunlestes* KIELAN-JAWOROWSKA, 1975

Type species: *Barunlestes butleri* KIELAN-JAWOROWSKA, 1975, the only species known.

Diagnosis and distribution. — See KIELAN-JAWOROWSKA 1975.

Barunlestes butleri KIELAN-JAWOROWSKA, 1975

1975. *Barunlestes butleri* KIELAN-JAWOROWSKA: 9, fig. 2B, pls. 5 and 6.
1979. *Barunlestes butleri* KIELAN-JAWOROWSKA; KIELAN-JAWOROWSKA: 7, figs. 4A, 5, 6, 7, 8A, 9A, 10A, 11A, 12A, 13A, 14A, pls. 1 : 1, 2, 4 : 1, 5, 6, 7 : 1, 8 : 1, 9 : 2, 10 : 1, 11 : 1, 2.
1980. *Barunlestes butleri* KIELAN-JAWOROWSKA; KIELAN-JAWOROWSKA and TROFIMOV: 167, figs. 1, 2, pls. 1—8.

Diagnosis. — See KIELAN-JAWOROWSKA 1975.

Material, measurements, description of the skull, lower jaw, endocranial cast and dentition. — See KIELAN-JAWOROWSKA and TROFIMOV 1980.

Discussion. — See KIELAN-JAWOROWSKA 1975 and KIELAN-JAWOROWSKA and TROFIMOV 1980.

Genus? *Daulestes* TROFIMOV and NESOV, 1979

Type species: *Daulestes kulbeckensis* TROFIMOV and NESOV, 1979.

Diagnosis, distribution and description. — See NESOV and TROFIMOV 1979.

Discussion. — TROFIMOV and NESOV (*in* NESOV and TROFIMOV 1979) described a new genus and species *Daulestes kulbeckensis*, based on single fragmentary right lower jaw with incomplete dentition, from the Late Turonian of the Central Kyzyl Kum Desert in Uzbek SSR, and assigned it to the Zalambdalestidae. As the specimen is incompletely known, its attribution to the Zalambdalestidae cannot be in my opinion demonstrated with any certainty, and therefore it is here only tentatively assigned to this family.

COMPARISONS

Entire skulls of Late Cretaceous therian mammals are known only in four eutherian genera from Mongolia: *Kennalestes*, *Asioryctes*, *Zalambdalestes* and *Barunlestes*. Those of *Kennalestes* and *Asioryctes* display many primitive features, regarded as symplesiomorphous therian character states (KIELAN-JAWOROWSKA 1981).

The Zalambdalestidae are in various respects more specialized than *Kennalestes* and *Asioryctes* (see KIELAN-JAWOROWSKA 1969, 1978, 1979, CROMPTON and KIELAN-JAWOROWSKA 1978) and their skulls (KIELAN-JAWOROWSKA and TROFIMOV 1980) show a mosaic of primitive and specialized characters. The primitive characters shared by *Kennalestes*, *Asioryctes* and the Zalambdalestidae are as follows: the inclination of the occipital plate upwards and forwards from the condyles; posterior position of f. ovale; large promontorium; relatively posterior position of the glenoid fossa, opposite the anterior half of the promontorium; long jugal, reaching back the glenoid fossa; medial position of the internal carotid artery; medial inflection of the angular process of the dentary.

The medial position of the internal carotid artery requires explanation. PRESLEY (1979) demonstrated on embryological evidence that in present-day mammals the internal carotid artery is a single vessel, which may move medially or laterally during the growth of the promontorium and may be placed either along its medial border, or cross the middle or lateral sides of the promontorium. In two latter cases this vessel is commonly called the promontory artery; the absence of a promontory artery in the oldest known skulls of eutherian mammals, in *Kennalestes*, *Asioryctes* and the Zalambdalestidae (see KIELAN-JAWOROWSKA 1981 and KIELAN-JAWOROWSKA and TROFIMOV 1980 for detailed discussion) supports PRESLEY's idea.

The features of specialization of zalambdalestid skulls, which differ them from those of *Kennalestes* and *Asioryctes* are, in addition to the differences in the dentition: greater size, a more elongated and tubular snout, a relatively shorter mesocranial region, a relatively more expanded brain case, the presence of a large posterior palatine foramen, the presence of a median process of presphenoid, a very large pterygoid process of basisphenoid, the absence of a basisphenoid wing, the presence of f. rotundum (which in *Asioryctes* in confluent with sphenorbital fissure), the absence of a Vidian foramen and lack of coronoid bone, a remnant of which is present in *Kennalestes* and *Asioryctes*.

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EXPLANATION OF THE PLATES 14—17

PLATE 14

Zalambdalestes lechei GREGORY and SIMPSON

Upper Cretaceous, Djadokhta Formation, Bayn Dzak, Gobi Desert Mongolia, ZPAL MgM-I/43 (see also pl. 15)

1a. Stereo-photograph of the fragment of rostrum, associated with right and left lower jaws in ventral view, × 2.
1b. The same in right lateral view, × 2.
1c. The same in left lateral view, × 2.
1d. Stereo-photograph of the same, after the separation of the lower jaws, in occlusal view, × 2.
1e. Scanning electron microscope stereo-photograph of the right P^4—M^3 in oblique postero-occlusal view, × 10.5.
1f. Scanning electron microscope stereo-photograph of the right P^4—M^2 in occlusal view, × 10.5.
1g. Scanning electron microscope stereo-photograph of the right P_4—M_1 in occlusal view, × 10.5.

Figs. 1a-d photo: M. Czarnocka
1e-g photo: G. R. Pierce

PLATE 15

Zalambdalestes lechei GREGORY and SIMPSON

Upper Cretaceous, Djadokhta Formation, Bayn Dzak, Gobi Desert, Mongolia, ZPAL MgM-I/43 (see also pl. 14)

1a. Left lower jaw without a ramus, with complete dentition, I_1, I_3 and C with tips broken off, in outer view.
1b. The same in inner view.
1c. Stereo-photograph of the same in occlusal view.
1d. Stereo-photograph of the right lower jaw of the same, without ramus, with complete dentition, but the tip of I_1 broken off, in outer view.
1e. Stereo-photograph of the same in occlusal view.
1f. Stereo-photograph of the same in inner view.

All × 4

Photo: M. Czarnocka

PLATE 16

Zalambdalestes lechei GREGORY and SIMPSON

Upper Cretaceous, Djadokhta Formation, Bayn Dzak, Gobi Desert, Mongolia

1a. The skull with badly damaged cranial roof, the anterior part of which has not been preserved and has been made of plastic. Of I_3 and C only the moulds have been preserved, which have been filled with plastic material, the sandstone surrounding them subsequently being removed. The endocranial cast is in the natural position, in which it has been preserved. Right lateral view, ZPAL MgM-I/16, × 5.
1b. Stereo-photograph of the same in occipital view, LMF — lower mastoid foramen, UMF — upper mastoid foramen, × 4.
2a. Stereo-photograph of the rostral part of the skull in oblique dorso-lateral view, showing olfactory bulbs and the orbit, ZPAL MgM-I/14, × 4.
2b. Stereo-photograph of the same in lateral view, showing the details of the orbit, MF — maxillary foramen, SPHF — sphenopalatine foramen, PPF — posterior palatine foramen, × 4.
2c. Stereo-photograph of the same in posterior view, showing (at the top) the olfactory bulbs in posterior view and (below) the posterior part of cribriform plate, × 4.

Photo: M. Czarnocka

PLATE 17

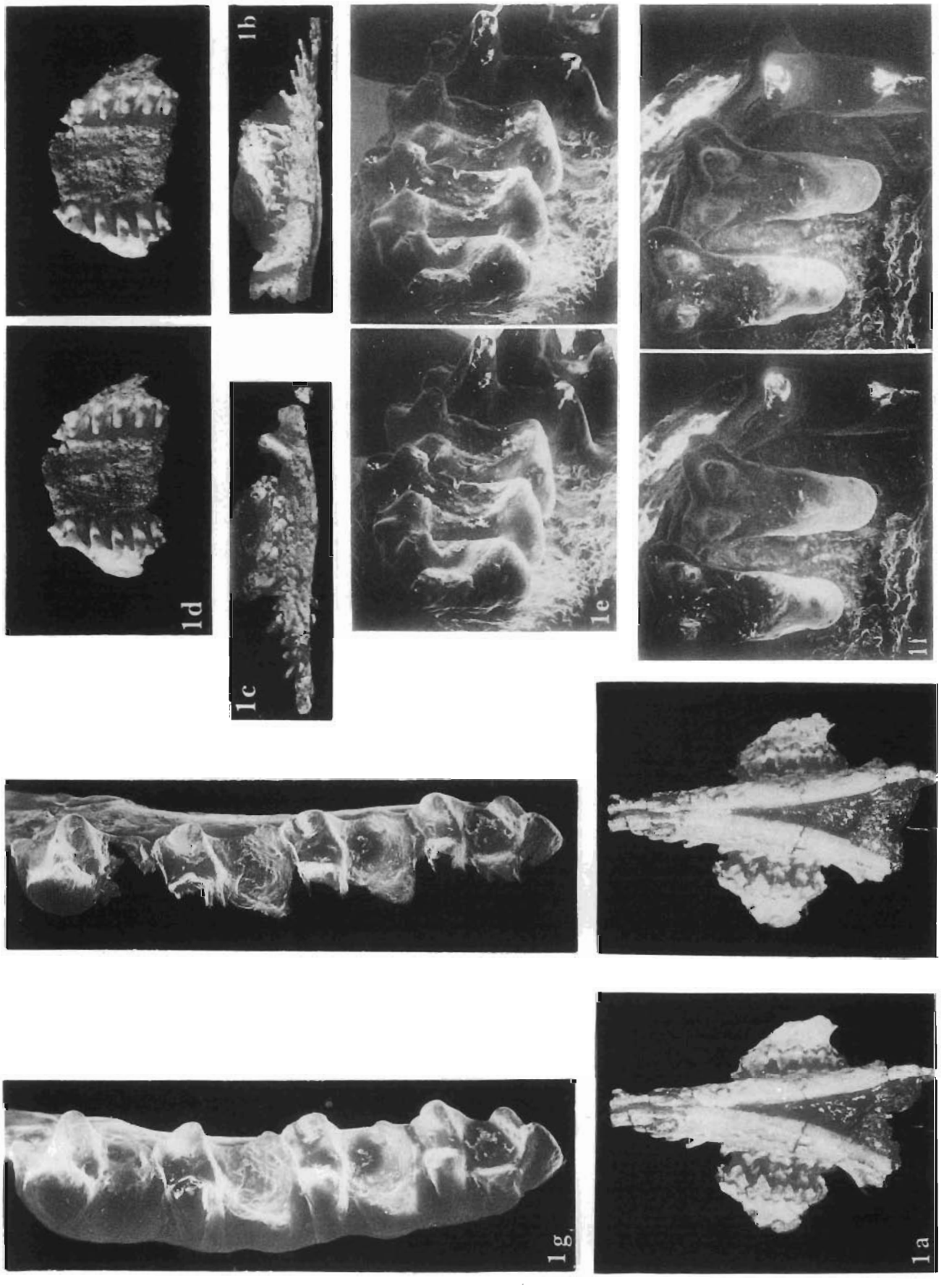
Zalambdalestes lechei GREGORY and SIMPSON

Upper Cretaceous, Djadokhta Formation, Bayn Dzak, Gobi Desert, Mongolia

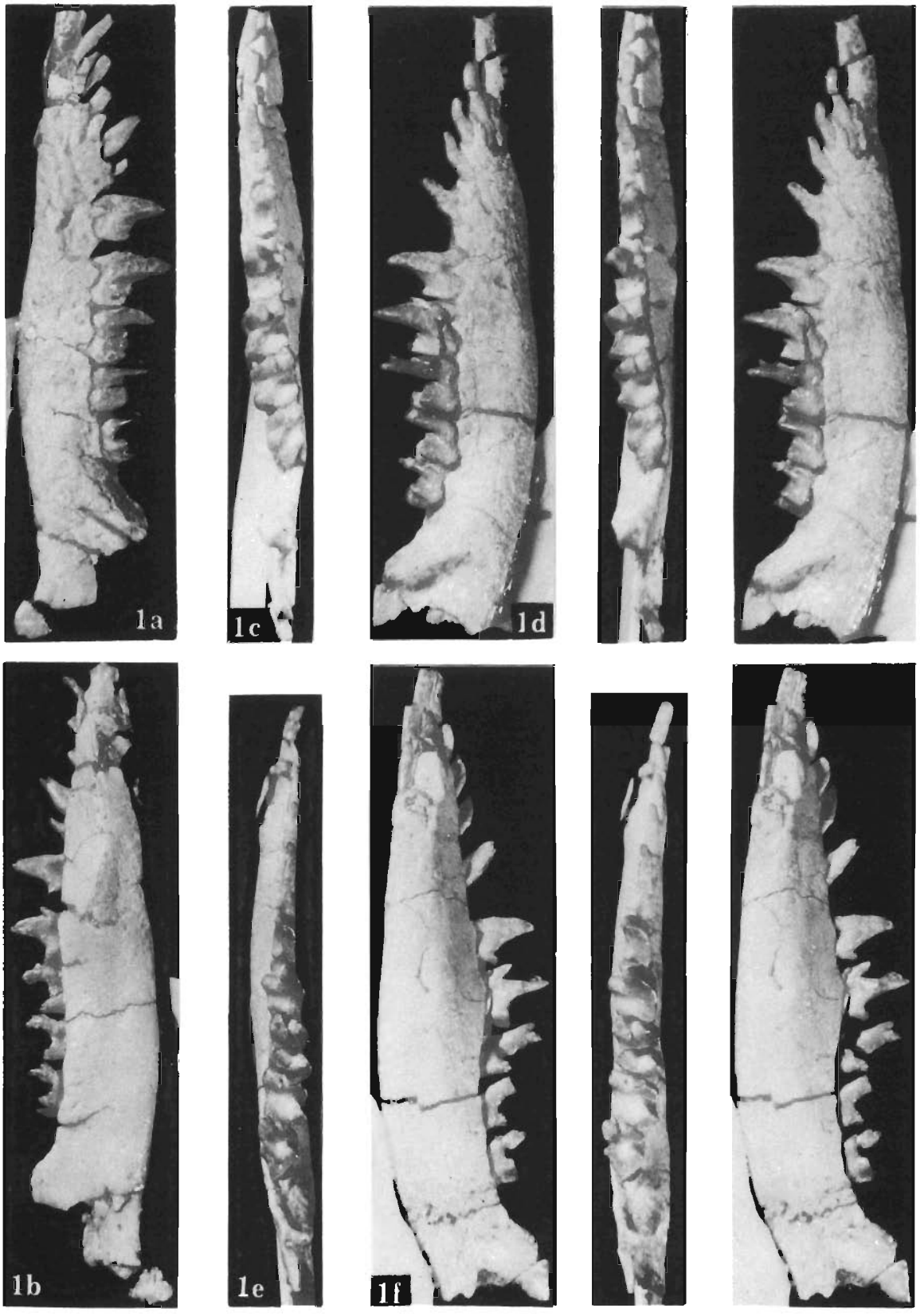
1a. Stereo-photograph of a badly damaged skull of an old individual in left lateral view, ZPAL MgM-I/13.
1b. Stereo-photograph of the same in occlusal view.
1c. Stereo-photograph of a badly damaged left lower jaw of the same individual in outer view.
1d. Stereo-photograph of the same in occlusal view.
1e. Stereo-photograph of the same in inner view.
1e. Stereo-photograph of the right lower jaw of the same individual in outer view.

All × 4

Photo: W. Skarżyński



Z. KIELAN-JAWOROWSKA: SKULL IN ZALAMBDALESTIDAE


1a
1c
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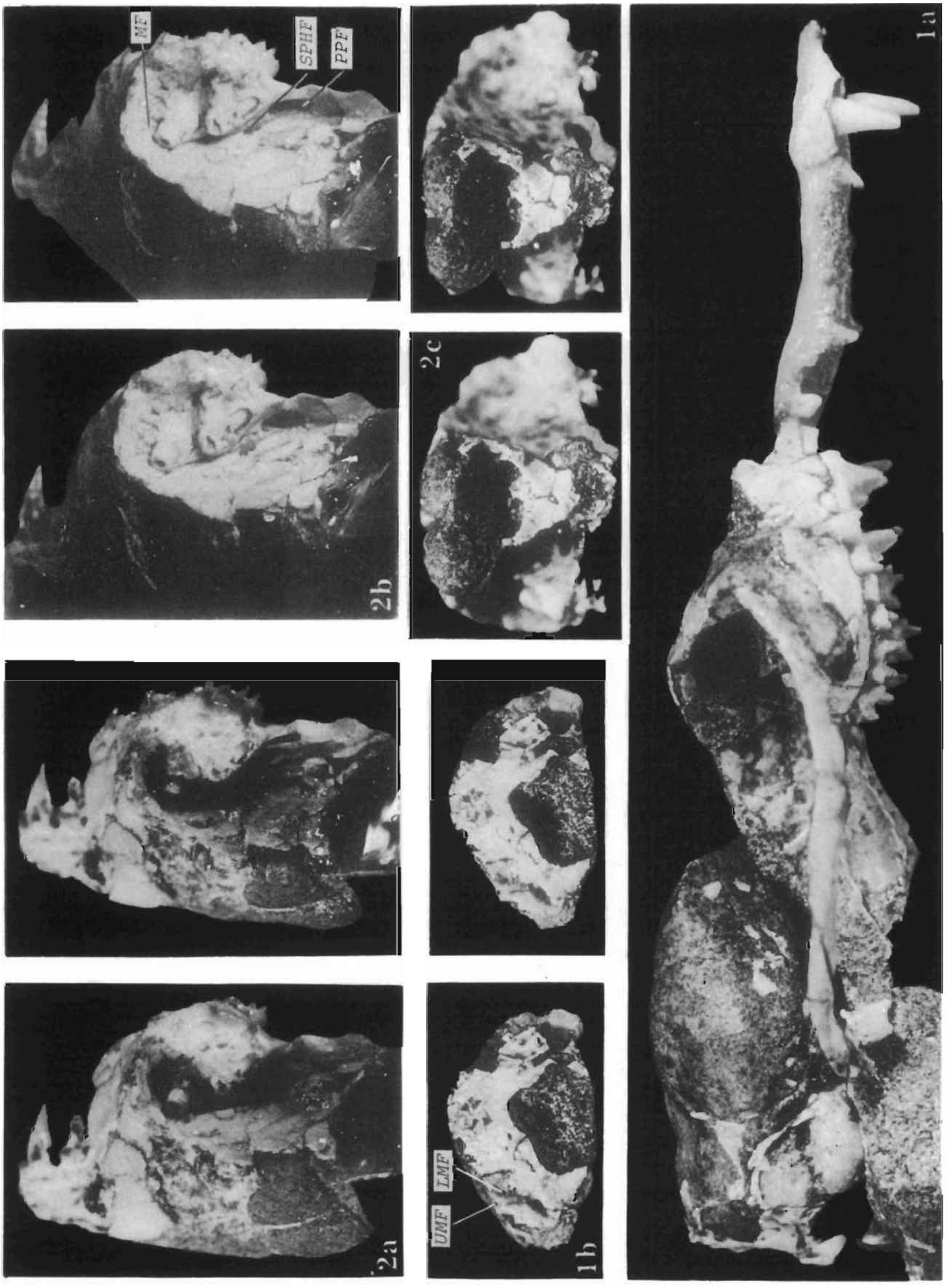
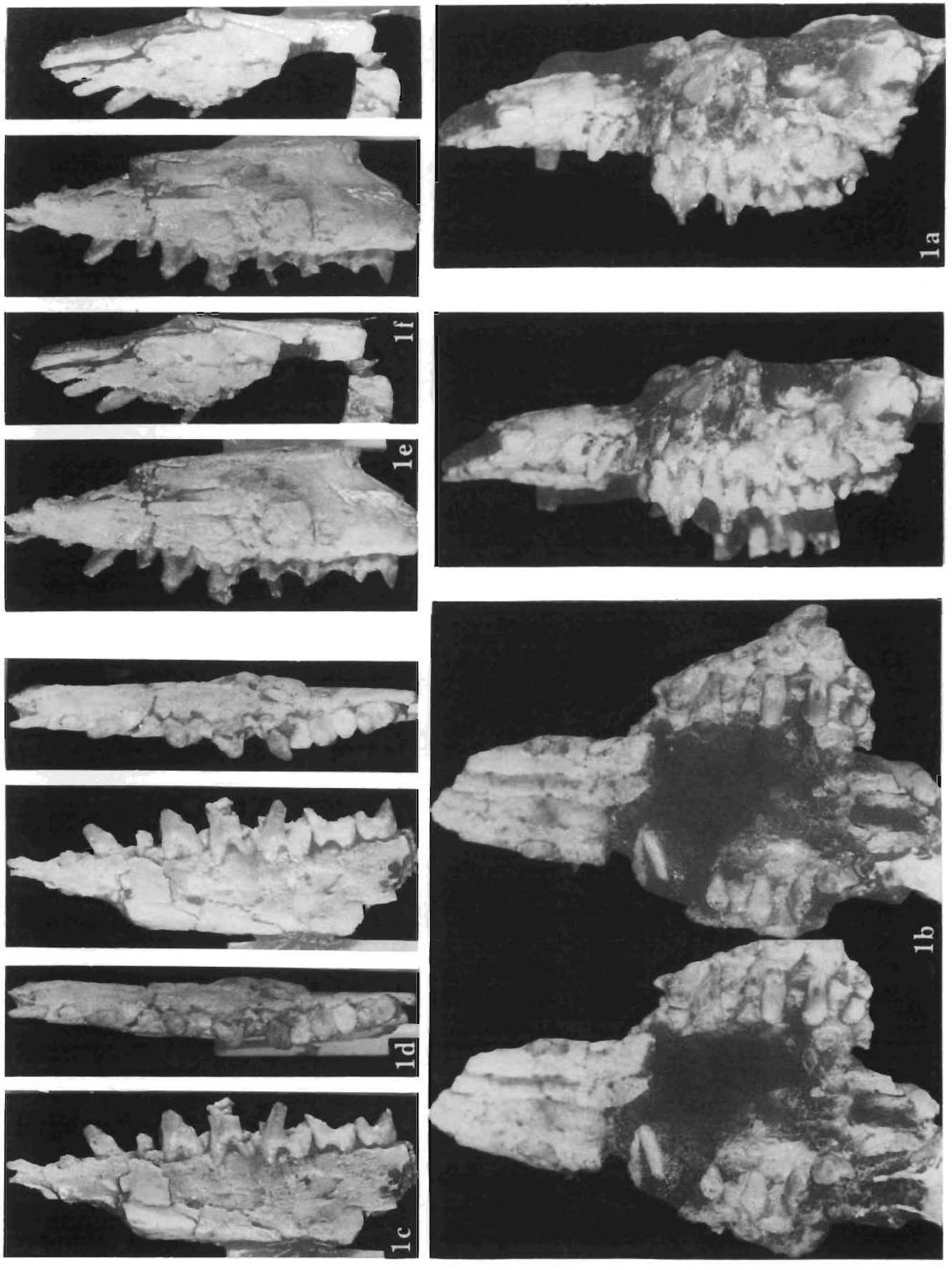


Z. KIELAN-JAWOROWSKA: SKULL IN ZALAMBDALESTIDAE



Z. KIELAN-JAWOROWSKA: SKULL IN ZALAMBDALESTIDAE